Patch-scale selection patterns of grazing herbivores in the central basalt plains of Kruger National Park

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ABSTRACT

Large herbivores form an essential component in the ecosystem, due to the impact that they have on their surrounding habitat. In this study we aimed to evaluate some of the mechanisms behind how herbivores select forage at a patch scale. Thirty-six experimental plots were established and fitted with camera traps in Kruger National Park to test forage selectivity by grazers. Plots were manipulated through clearing with a brush cutter, and the application of fertiliser. We used generalised linear models to detect trends in probability of occurrence by seven grazing herbivore species using camera trap data. Our results showed that season was a major determinant of species distribution, especially those which are not obligate grazers or feed exclusively in the 0.5 km to 2 km zone from water. We found that most selective feeding occurred in the late wet season when water would be more evenly distributed across the landscape and forage resources close to water would have had the chance to recover from depletion as a result of dry season use. This has implications for the distribution of artificial water points across the landscape, as areas of reserve forage must be maintained to alleviate grazing pressure close to water.

Key Words: extrinsic drivers, forage selection, herbivore distribution, intrinsic traits, water availability, African elephant, African buffalo, White rhino, Blue wildebeest, Plains zebra

INTRODUCTION

Large mammalian herbivores form an essential component of the ecosystem in which they occur, due to the impact that they have on its structure and function (Hempson *et al.,* 2015). Grazing herbivores, in particular, engineer their surrounding ecosystem through enabling plant succession and promoting grassland diversity (Olff & Ritchie, 1998). Furthermore, they develop and maintain key resource areas (McNaughton, 1984), facilitate for other selective grazers (Prins & Ollf, 1998) and provide ephemeral nitrogen pulses to vegetation through processes of dunging and soil leaching (Frost & Hunter, 2007). Because of the effects which herbivores have on the ecosystem, understanding habitat selection and patch scale foraging processes is becoming increasingly important. Grazing habitats in Africa are under threat as C_4 grasses (which are dominant across savannas) decrease with increasing CO_2 levels (Bond, 2008), and the patch scale foraging patterns of herbivores significantly affect landscape scale processes (Shipley, 2007). Herbivores select for the habitat in which they feed over several temporal and spatial scales (Bailey *et al.*, 1996), under the constraints of their morphology – body size (Clauss *et al.*, 2003), mouth morphology (Pretorius *et al.*, 2016), dietary preference (Gordon & Illius, 1996; Hempson *et al.,* 2015), digestive strategy (Gagnon & Chew, 2000) and water-dependency (Hempson *et al.*, 2015).

Body size constrains digestive requirements in that larger species require more total energy than smaller species, but smaller species require more energy relative to their body weight than larger species (Demment *et al.*, 1985). Thus, smaller grazers experience greater digestive constraints than larger grazers (Codron *et al.*, 2007) and must extend a larger search effort in order to obtain high quality forage (Bailey *et al.*, 1996). Larger grazers are able to maximise their forage consumption through high intake of low-quality forage, particularly in the dry season when high quality forage is limited (Demment *et al.*, 1985; Owen-Smith *et al.*, 2017). Digestive strategy further alters the efficiency with which herbivores meet metabolic requirements, as non-ruminants experience an increased turnover rate in digestion which allows them to tolerate higher fibre and lower nutrition content than ruminants (Clauss *et al.*, 2003; Duncan *et al.*, 1990). In order to meet nutritional requirements within the constraints of morphology, herbivores have adapted mouth structures which optimise rate of forage intake (Shipley, 2007). For this reason, grazers tend to have wider muzzles and incisor arcades than browsers (Gordon & Illius, 1988), allowing higher bite rates (Pretorius, 2009). Within the grazer guild, variation in muzzle width occurs to allow maximum nutrient intake based on digestive strategy and metabolic requirements, and as such the scaling between muzzle width and body size governs grass height selection (Arsenault & Owen-Smith, 2008). However, the relationship between body size and tolerance for low quality forage is not strictly linear (Clauss and Hummel 2005) and is better explained by constraints in forage quantity and quality (Owen-Smith *et al.*, 2017).

Energy and nutrient intake of large herbivores influence their functional response and is determined by the time they spend feeding and the forage they consume (Spalinger and Hobbs 1992). Changes in plant phenology as well as individual forage demand, due to growth, reproduction or lactation, affects seasonal forage and habitat selection (Wilmshurst et al. 2000). For example, herbivores may select short, high-quality patches when they have greater demands for nutrients and energy, such as during the wet season when they are growing and lactating (Wilmshurst et al. 2000, Arsenault and Owen-Smith 2008). Within the constraints of physiognomic requirements, herbivores must use their daily activity budgets to select habitat which provides optimal forage and facilitate the evasion of predators (Owen-Smith & Goodall, 2014, Brooke et al. 2020). As such, herbivore populations are regulated by top-down processes (predation) in which case they need to minimize mobile activity; or bottom-up processes (forage quality and availability) for which they need to maximize foraging time (Hopcraft *et al.*, 2010; Owen-Smith *et al.*, 2014). Body size interacts with risk of predation, and in areas of diverse herbivore and predator body size, smaller herbivores experience a greater risk of predation than larger herbivores, as both small and large predators can consume small-bodied prey (Hopcraft *et al.*, 2010). Furthermore, behaviour of species (e.g. gregariousness) affects predator-avoidance strategies and determines whether herbivores may select more open or dense habitats (Riginos & Grace, 2008). The underlying environmental gradients: soil, climate, water availability and their subsequent effect on forage quality and quantity, provides structure to the landscape. This determines herbivore abundance and distribution across the landscape within the constraints of bottom-up and top-down processes (Bailey *et al.*, 1996; Hopcraft *et al.*, 2010). Forage quality is additionally affected by nutrient content of the soil, (Holland & Detling, 1990), season, regrowth as a response to herbivory and/or fire, and water availability (Wilsey, 1996). Water availability strongly constrains the distribution and abundance of grazers through its effects on forage quality and quantity, and high water dependency experienced by grazers (Hempson *et al.,* 2015).

There is complexity and a high degree of interaction between these processes, which operate differently under a variety of scales. At a landscape scale, water availability, foraging requirements and predator distribution and activity patterns determine abundance and distribution of herbivores (van Ginkel *et al.*, 2018). At a patch scale, perceived risk of predation and selective foraging alters herbivore behaviour (Riginos *et al.*, 2008; van Ginkel *et al.*, 2018); and ultimately these patch processes determine landscape heterogeneity. The complexity and degree of interactions between these processes highlights the importance of understanding savanna ecology to management. Conservation management interventions, such as artificial water provision, without full comprehension of these interactions can have unintended consequences.

Kruger National Park, hereafter 'KNP', has throughout its history altered its management approaches, and has contributed substantially to the understanding of savanna ecology through the monitoring and research of their management efforts (Biggs, 2003). The study of patch scale selection processes in KNP is facilitated by the heterogenous landscape, which supports diverse herbivore assemblages. Patch scale foraging processes have significant impacts on large scale distribution patterns of herbivores (Shipley, 2007). Due to the associated effects that herbivore presence has on the environment, understanding patch scale selection is important to the prediction of their presence, and thus for the purpose of their management (Pretorius, 2009). This study aims to evaluate the mechanisms behind patch scale habitat selection by a variety of grazing species across a spectrum of body sizes and differing digestive strategies. We used descriptions of feeding preference, digestive strategy, body size, mouth morphology and water-dependency to describe patch selection in seven grazer species at the Satara section of KNP. We tested habitat attributes against species probability of presence at a patch-scale by manipulating plots to test if; a) season would have a strong effect on grazer presence at certain distances to water b) selectivity by species would change across seasons; c) risk of predation would influence probability of small grazer presence more than large grazer presence.

MATERIALS AND METHODS

Study area

This study was conducted in the Satara section (central basalt plains) of KNP, which is situated at the north-eastern corner of South Africa (24.01°S, 31.49°E). Satara receives a mean annual rainfall of 547 mm (February *et al.*, 2013). The region experiences mean minimum temperatures of 10°C and 20°C, and mean maximum temperatures of 26.3°C and 32.6°C in July and December respectively (Parr, 2008). The vegetation is characterised by *Senegalia nigrescens/Sclerocarya birrea* tree savanna (Gertenbach, 1983). Habitats of this area are attractive to grazers as the N'wanetsi and Sweni rivers typically flow once or twice in the wet season and have a number of pools which may persist in the dry season (Gaylard *et al.*, 2003). Furthermore, surface water takes longer to evaporate on the clayey basaltic soils of the region, resulting in water being more locally available across the landscape in the wet season in the form of pans (Gaylard *et al.*, 2003). The Letaba basalt soil type contributes to study area suitability, as it has higher calcium carbonate ($CaCo_3$) concentrations, which gives rise to extensive grassy plains (Venter, 1986) that are dominated by highly palatable grass species such as *Urochloa mosambicensis* and *Digitaria eriantha* (O'Connor & Pickett, 1992*)*. The area is also exposed to occasional wild-fires and prescribed burns (Van Wilgen *et al.*, 2004).

Site design

Suitable sites were identified by mapping distance to water as buffers of 0.5 km, 2.5 km and 5 km from all surface water (rivers and artificial waterholes), overlaid across the soil and habitat type layers using ArcGIS v10.5 (ESRI, 2012). Site suitability was characterised by relative distance to water, soil type, habitat type, accessibility (distance from road in order to ease carrying of equipment) and the absence of previous experimental manipulation. Sites

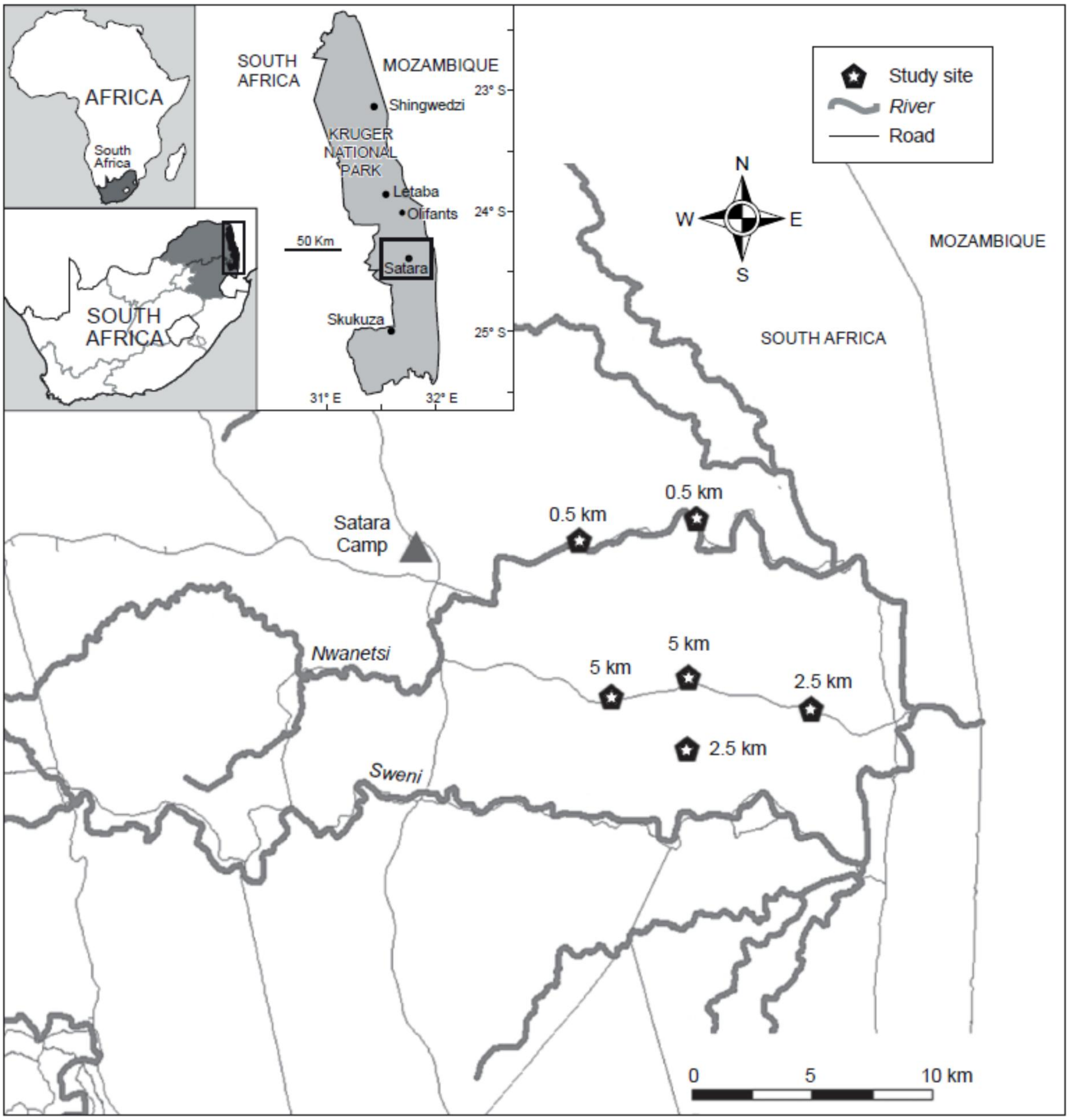

Figure 1: Map of the Satara section where the study was conducted, relative to the Satara Rest Camp.

were replicated at a location > 2 km away from each other, hence six sites were studied in total (Fig. 1 and 2). Sites were located at three different distances to water, with sites 0.5 km from water situated north of the N'wanetsi river and those 2.5 km and 5 km from water south of the N'wanetsi river. Five of the six sites fell within the Satara land type in KNP, dominated by *Senegalia nigrescens/ Sclerocarya birrea* tree savanna (Gertenbach, 1983), but due to constraints of site suitability one of the six sites fell within the Mavumbye habitat type, characterised as *Senegalia nigrescens* bush savanna (Gertenbach, 1983). Sites were sampled in June 2017 (site preparation), October 2017, February 2018 and June 2018, resulting in three sets of seasonal data, namely 'late dry', 'early wet' and 'late wet' seasons. Wildfires occurred throughout the sampling period, resulting in one site at 2.5 km burning in June 2017, and both 5 km sites burning in November 2017.

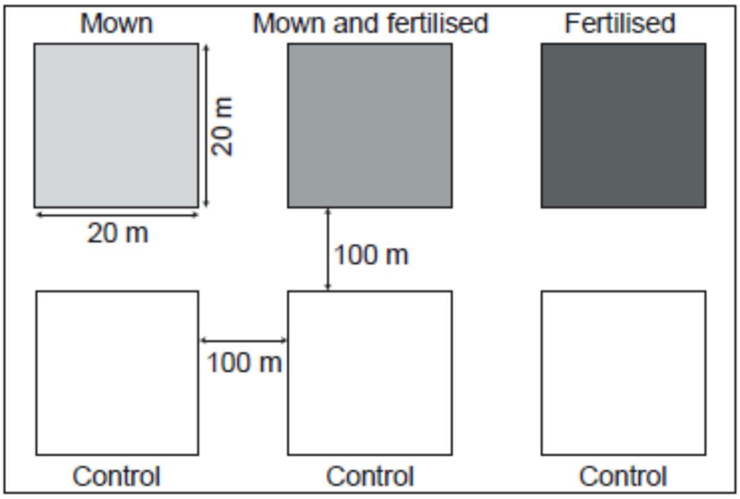

Figure 2: A visual representation of the plot layout at each of the six sites. Plots were 20 m x 20m ($400m^2$) and were set up approximately 100 m apart.

At each site, six experimental plots were established at a patch level scale (Fig. 2)- an area that an herbivore interacts for 1-30 min, takes breaks in foraging and would be affected by forage abundance and quality, plant species and social interactions (Bailey *et al.*, 1996). For this study, patch level scale refers to the 400 m^2 plot. Three of the six plots at each site were controls and three underwent the following treatments respectively: removal of the above-ground biomass layer through brushcutting; removal of the above-ground biomass layer through brushcutting and application of fertiliser; and application of fertiliser. Each plot was 400 m^2 and plots were approximately 100 m apart at each site. At mown plots, small woody shrubs above 1 m were not removed, and plots with little woody biomass were selected for.

At fertilised plots, 4 kilograms (kg) of 28% LAN/KAN N fertiliser and 3.2 kg of 14% Carbon-enriched, slow-release N fertiliser was applied evenly (Scientific Services recommendation, pers. com., 2017). Sites were evaluated two weeks before each data collection period to determine whether retreatment was necessary. Lack of rainfall in the dry season resulted in a limited increase of grass height regrowth of the treated plots, and thus the sites were not mown in October 2017, however fertiliser was reapplied. The full treatment was conducted again in February 2018. Overall, monthly rainfall was below average for all months except October 2017 across the duration of the study, which would likely have affected absorption of fertiliser applied in June 2017 and February 2018.

Each plot were fitted with a Cuddeback Attack Interchangeable Flash (Blue Series, Model 1255) camera trap. Camera trapping is an effective, non-intrusive and replicable means of surveying mammals over a wide range of environmental and temporal scales (Carbone *et al.*, 2001), allowing a novel means to overcome observational error of dung counts or animal observation counts. Camera traps were fitted to each plot to have the best visual of the 400m^2 plot area and were placed between 0.5 m and 1 m from the ground. They were angled away from the sun where possible, and set to a wide view angle, Fresnel cover lowered and aspect wide. The Camera traps were set to take photographs at 10-minute intervals when activity was sensed. Finally, they were serviced (batteries replaced, and data retrieved) every three months, but batteries lasted on average five weeks, resulting in five weeks of data per season.

Herbivore species

This study assesses the patch scale selection processes which grazers and mixed feeders undertake when foraging within the constraints of water availability, forage quality and quantity and habitat requirements using camera trap captures. We thus focused on nine commonly occurring grazer and mixed feeder species in the Satara region of KNP. These species were selected due to their representation of a suite of digestive strategies, feeding preferences and body sizes. The selected species were: five grazers (Burchell's zebra *Equus quagga* , waterbuck *Kobus ellipsiprymnus* , blue wildebeest *Connocheates taurinus*, buffalo *Syncerus caffer*, white rhinoceros *Ceratotherium simum*); and two mixed feeders (elephant *Loxodonta africana* and impala *Aepyceros melampus*). Attributes assigned to camera trap data were as follows: date; species within the photo; time of day; functional characteristics (body size, feeding preference and digestive type), hereafter 'functional types', and number of individuals. Feeding preference followed the generalist functional classifications of grazing and mixed feeding ungulate herbivores described by Owen-Smith (1982).

Environmental covariates

Distance to water was the primary determinant of site placement as it typically dictates herbivore movement (Gaylard *et al.*, 2003) and seasonal population fluctuations of herbivore species. The distance from the N'wanetsi and Sweni rivers, and the associated waterholes of the area, were used to determine suitable sites of the three distances from water. Predation was measured through camera trap data, allowing covariates of predator species, incidences of multiple predators and days since predator presence to be measured. Lions were also recorded as an individual variable due to the strong influence they have across the spectrum of herbivore body sizes (Valeix *et al.*, 2009). Camera trap data additionally used to determine grass height (using a marked pole in front of each camera), and plot burn data (burnt/unburnt and days since fire).

The average distance to the nearest visual obstruction was measured as a proxy for landscape of fear, given that distance to the nearest obstruction changes ambush risk by a predator and anti-predator strategies by herbivores (Riginos, 2015). This value was the mean of measurements to the nearest obstruction (trees or shrubs) from the middle of each plot, using a range finder at a height of 1.5 m every 15 degrees, totalling 24 measurements (Riginos, 2015). The inverse of these measures was used to determine the distance between trees.

The following environmental variables were taken on each plot at each data collection period to measure forage quantity and quality: grass biomass using a disc pasture meter (Trollope & Potgieter, 1986), for which the measurement value was used as a proxy for biomass; grass quality using ‘vigorous grass cover’ as a proxy (Venter and Watson 2008) estimated by the Walker 8-point scale (Walker, 1976); and grass species were identified and a percentage cover within the plot estimated using Braun-Blanquet measure (Westhoff & Van Der Maarel, 1978). Grass quality and percentage cover were estimated in a 1 m^2 grid which was dropped at 10 random points in the plot. The percentage of vigorous grass cover was determined using the mean of ‘vigorous’ values determined using the Walker 8-point scale (Walker, 1976). The coefficient of variation (CV) for grass biomass values was used as a measure of biomass heterogeneity, and the CV of distance to the nearest obstruction as landscape heterogeneity.

Data analysis

Data were split into five time classes, namely: ‘pre-sunrise’ (00h00 to 05h59), ‘morning’ (06h00 to 09h59), ‘midday’ (10h00 to 13h59), ‘afternoon’ (14h00 to 17h59) and ‘night’ (18h00 to 23h59). Camera trap captures for each treated plot were recorded individually, however control plot data for the respective site was grouped together. Each capture was recorded as detection/non-detection irrespective of number of individuals in the capture, to determine probability of a species occurring at a site. To determine which environmental variables had the strongest effect on plot selection by species, daily time of day binomial values were tested

Table 1: Study species characters and the predictions of expected model outcomes based on the effect of environmental variables on these characteristics. Species traits were based off the following literature: Gagnon *et al.,* 2000; Clauss *et al.,* 2003; Hopcraft *et al.,* 2010; Hempson, Archibald *et al.,* 2015.

Species	Characteristics	Prediction
Impala	Small-medium mixed feeder (browser-grazer intermediate), ruminant, selective feeder, water dependent	Alters distribution in response to water availability across seasons by moving closer to water in the dry season, responds to mown, mown and fertilised treatments, responds to risk of predation.
Wildebeest	Medium grazer, ruminant, selective feeder (variable grazer), water dependent	Alters distribution in response to water availability across seasons by moving closer to water in the dry season, responds to mown, mown and fertilised treatments, responds to risk of predation.
Waterbuck	Medium-large grazer, ruminant, selective feeder (variable grazer), water dependent	Remains closer to perennial water sources throughout in the dry and wet season, responds to mown, mown and fertilised treatments, responds to risk of predation.
Zebra	Medium-large grazer, non-ruminant, non-selective feeder (obligate grazer), water dependent	Alters distribution in response to water availability but will trade-off feeding close to water to obtain a higher quantity of forage. Responds to fertilised treatments in the dry season and mown and fertilised treatments in the wet season. Less responsive to risk of predation.
Buffalo	Large grazer, ruminant, non-selective feeder (variable grazer), water dependent	Alters distribution in response to water and forage availability. Trade-off being close to water to obtain high quantity forage, responds to fertilised treatments in both the dry and wet season. Less responsive to risk of predation.
Elephant	Megaherbivore mixed feeder (browser-grazer intermediate), non-ruminant, non-selective feeder, water dependent	Alters distribution in response to water and forage availability, will occur further from water to obtain high quantity forage. Unlikely to respond to treatments, will not respond to risk of predation.
White Rhinoceros	Megaherbivore selective feeder (obligate grazer), non-ruminant, water dependent	Remains closer to perennial water across seasons, responds to mown, mown and fertilised treatments across seasons, will not respond to risk of predation.

against environmental covariates using a generalised linear model in R v3.4.1 (R-Development-Core-Team, 2011). We used the Akaike Information Criterion (AICc) (library AICcmodaavg in R) to inform which model most suitably described the probability of a species selecting a plot to forage. Using literature, we developed predictions (Table 1) of what environmental variables would result in the lowest AICc value for each species and wrote a model to test these predictions. Thirty-four plausible models were then constructed, and each species was tested against the prediction model for each species; and the AICc values of the prediction model compared to the plausible model results. For species which had low capture rates over the data collection period, models were restricted to additive models rather than interactive models, as we had a set of variables against which to test species detection, and interactions between these variables could not be tested due to small sample size. The temporal resolution of the data did not allow us to test the effects of predation against time of day, and as such predation was not included as a variable in the models.

RESULTS

For most species, the predictive models had higher AICc values than the plausible models against which they were tested (Appendix A). This is likely because the predictive models that were written had few variables and were thus not explanatory enough of species patterns. Species with low detection data typically experienced more specialised feeding requirements, and as such trends at all treatments and/or all distances from water cannot be represented in the figures.

Table 2: the results of model outcomes with the lowest aICc value for each species across the seasons (late dry, early wet and late wet) and three distances to water (0.5 km, 2.5 km and 5 km). For treatment, ‘M’ refers to mown plots, ‘MF’ refers to mown and fertilised plots and ‘F’ refers to fertilised plots, ‘ + ’ represents a preference for the treated plot and ‘–’ represents a preference for the control plots. ‘X’ represents effects that could not be detected, either, because results between treated and control plots did not differ significantly, or, because the effect could not be tested, because of a small sample size.

				Response						Response	
Species	Season	Treatment	0.5	2.5	5	Species	Season	Treatment	0.5	2.5	5
Impala	Late dry	M	+	+	-	*Buffalo*	Late dry	M	x	+	-
		MF	-	-	+			MF	x	+	+
		F	-	-	-			F	x	-	-
	Early wet	M	+	+	+		Early wet	M	x	+	+
		MF	+	-	-			MF	x	-	-
		F	-	-	-			F	x	-	-
	Late wet	M	-	-	-		Late wet	M	x	-	-
		MF	+	+	+			MF	x	x	-
		F	-	-	-			F	x	+	+
Wildebeest	Late dry	M	-	+	+	*White rhinoceros*	Late dry	M	x	x	x
		MF	-	-	-			MF	x	x	x
		F	+	-	-			F	x	x	x
	Early wet	M	-	-	+		Early wet	M	x	x	x
		MF	-	-	-			MF	x	x	x
		F	-	-	-			F	x	x	x
	Late wet	M	-	-	-		Late wet	M	x	x	x
		MF	+	+	-			MF	x	x	x
		F	-	-	+			F	x	x	x
Waterbuck	Late dry	M	+	+	x	*Elephant*	Late dry	M	x	x	x
		MF	-	-	x			MF	x	x	x
		F	-	-	x			F	x	x	x
	Early wet	M	+	+	x		Early wet	M	x	x	x
		MF	-	-	x			MF	x	x	x
		F	-	-	x			F	x	x	x
	Late wet	M	+	+	x		Late wet	M	x	x	x
		MF	-	-	x			MF	x	x	x
		F	-	-	x			F	x	x	x
Zebra	Late dry	M	-	-	-						
		MF	-	-	-						
		F	+	+	+						
	Early wet	M	-	-	-						
		MF	-	-	-						
		F	-	-	-						
	Late wet	M	-	-	-						
		MF	-	+	+						
		F	-	-	-						

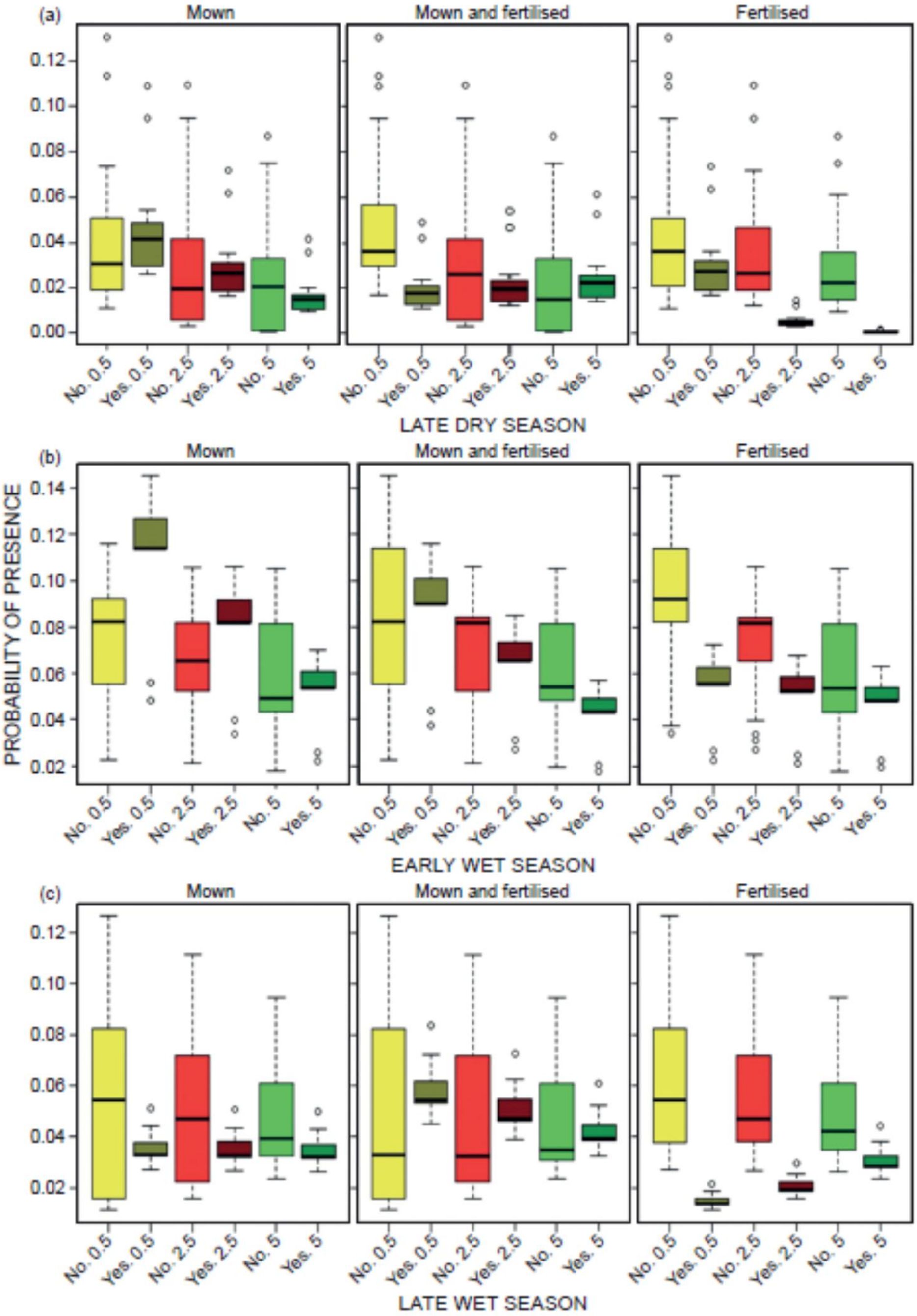

Figure 3: Results from lowest aICc value models for impala across distance from water throughout the three sampling seasons. 'No: 0.5' represents probability of presence for the species at untreated sites at 0.5 km from water and 'Yes: 0.5' represents the respective treatment at 0.5 km from water. the three distance values are 0.5 km from water, 2.5 km from water and 5 km from water. the graphics have been rescaled to be clearly interpreted and therefore probability values are not shown on a full axis (i.e. 0–0.1 probability of presence)

Impala

In the late dry season, preference was shown for mown sites closer to water (0.5 km and 2.5 km), and for mown and fertilised sites furthest from water (5 km) (Table 2, Fig. 3.). In the early wet season, preference was shown for mown plots at all three distances to water, and at the mown and fertilised plot at 0.5 km from water. In the late wet season, preference was shown for mown and fertilised plots at all distances from water. No preference was shown for fertilised treatments across all three seasons.

Waterbuck

Across all three seasons, preference was shown for mown plots at 0.5 km and 2.5 km from water (Table 2, Fig. 4). Waterbuck did not respond to any other treatments and were not detected 5 km from water.

iIdebeest

In the late dry season, preference was shown for mown plots further from water (2.5 km and 5 km), and fertilised plots closer to water) (Table 2, Fig. 5). In the early wet season, preference was shown for mown plots furthest from water. In the late wet season, preference was shown for mown and fertilised plots closer to water (0.5 km and 2.5 km), and fertilised plots furthest from water.

Zebra

In the late dry season, zebra responded to fertilised plots at all three distances from water (Table 2, Fig. 6). In the early wet season, they did not show a response to any treatment at any distance from water. In the late wet season, zebra showed preference for mown and fertilised plots further from water (2.5 km and 5 km).

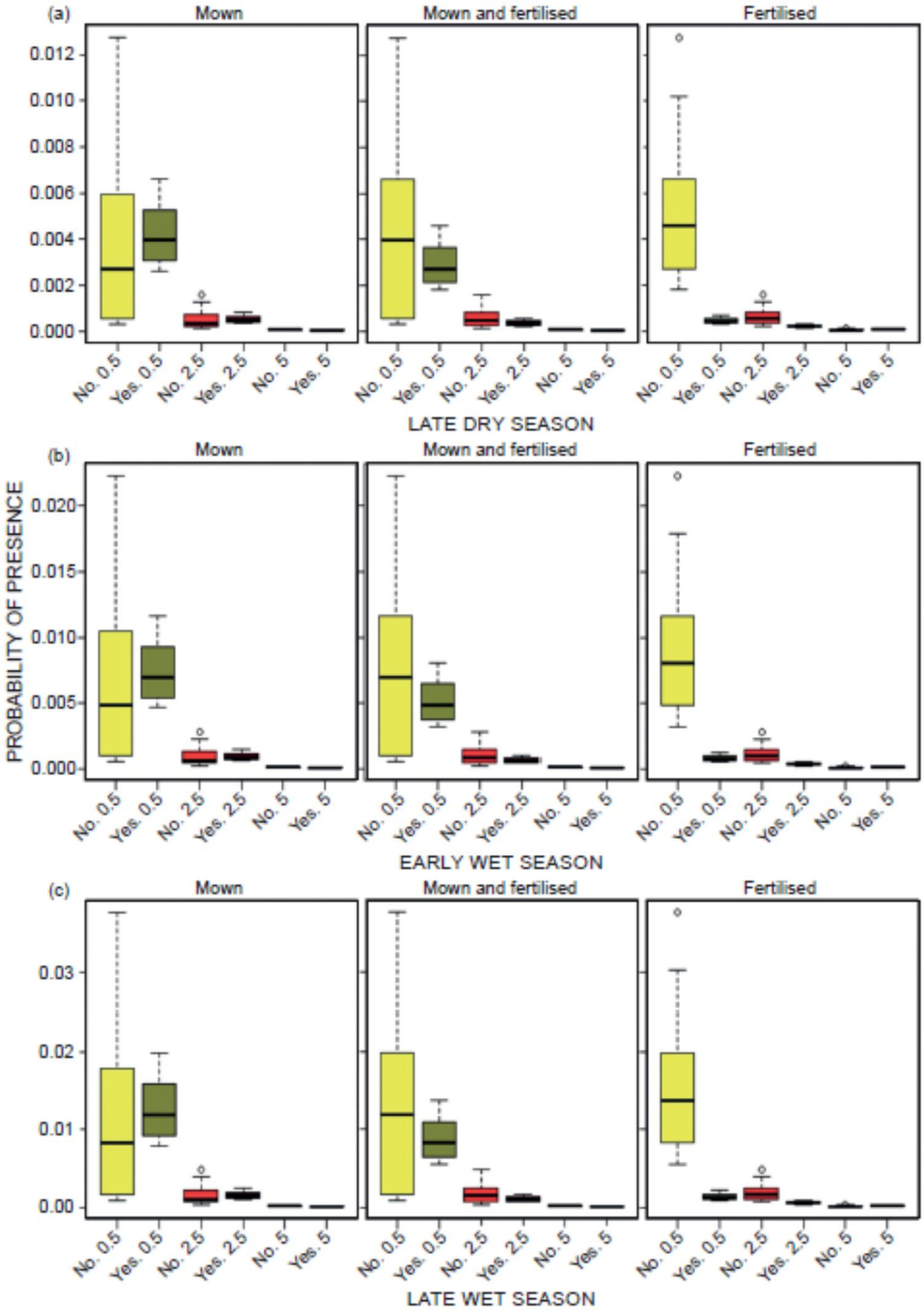

Figure 4: Results from lowest aICc value models for waterbuck across distance from water throughout the three sampling seasons. 'No: 0.5' represents probability of presence for the species at untreated sites at 0.5 km from water and 'Yes: 0.5' represents the respective treatment at 0.5 km from water. the three distance values are 0.5 km from water, 2.5 km from water and 5 km from water. the graphics have been rescaled to be clearly interpreted and therefore probability values are not shown on a full axis (i.e. 0–0.1 probability of presence)

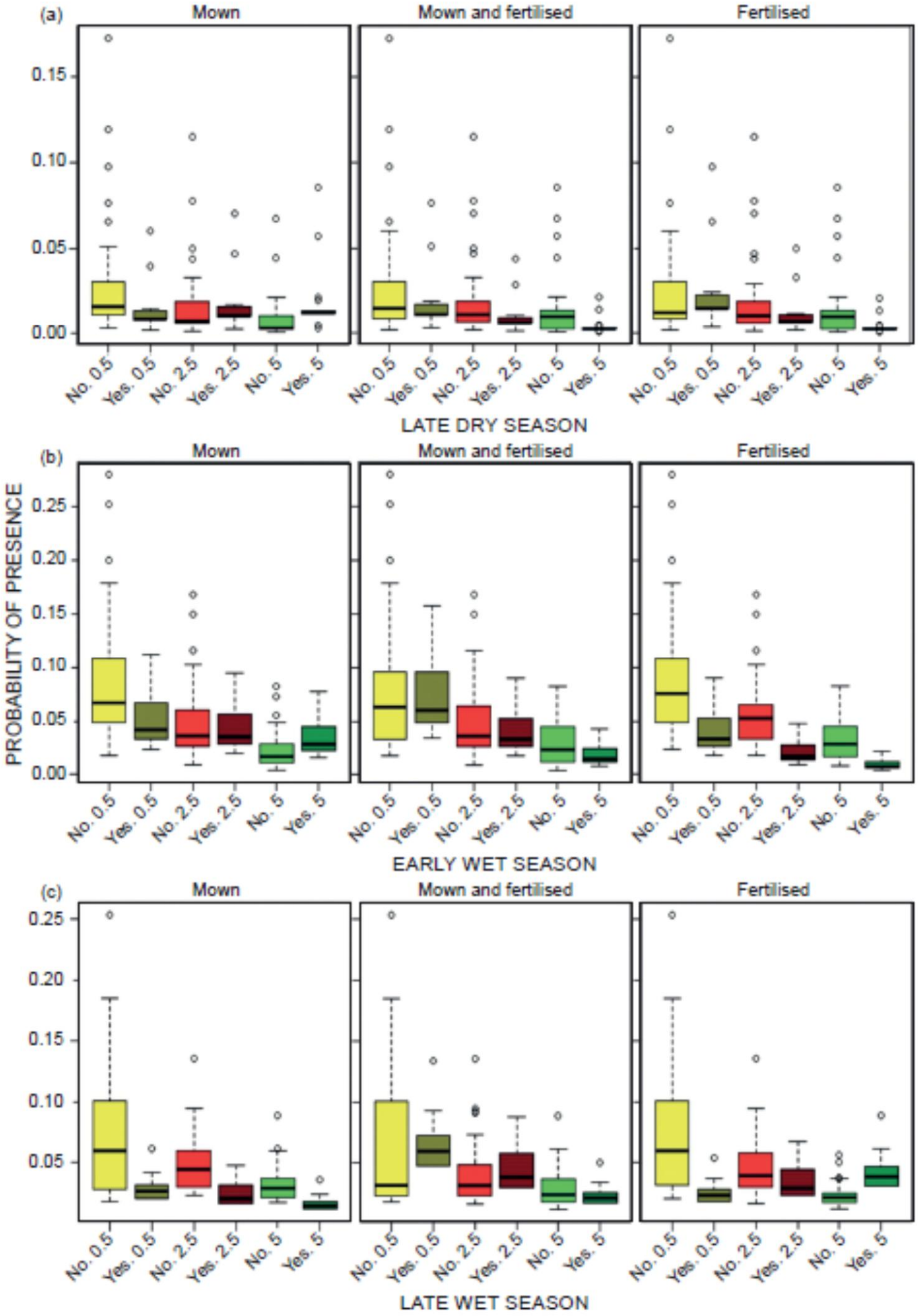

Figure 5: Results from for lowest aICc value models for wildebeest across distance from water throughout the three sampling seasons. 'No: 0.5' represents probability of presence for the species at untreated sites at 0.5 km from water and 'Yes: 0.5' represents the respective treatment at 0.5 km from water. the three distance values are 0.5 km from water, 2.5 km from water and 5 km from water. the graphics have been rescaled to be clearly interpreted and therefore probability values are not shown on a full xis (i.e. 0–0.1 probability of presence)

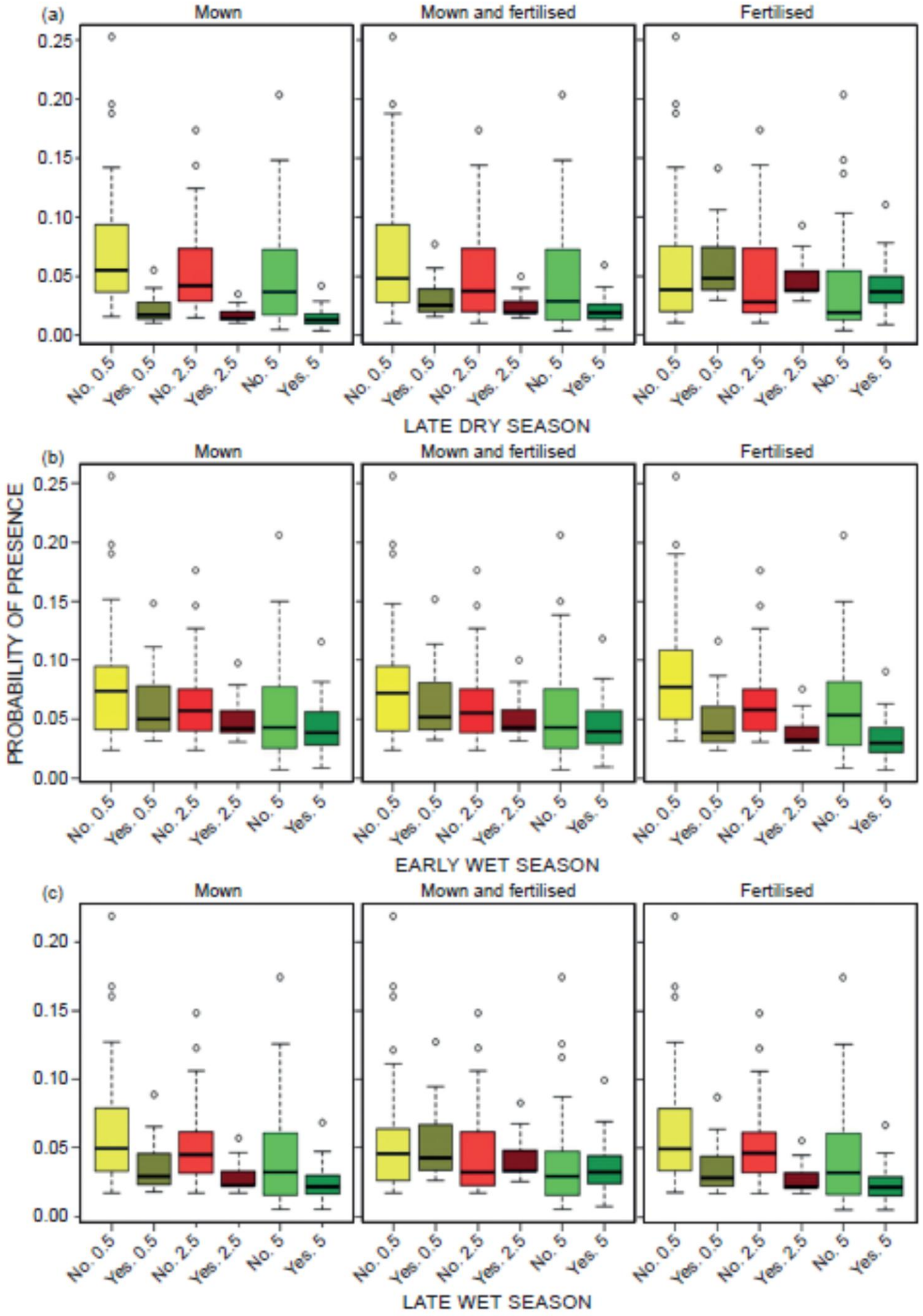

Figure 6: Model results for lowest aICc value models for zebra across distance from water throughout the three sampling seasons. ‘No: 0.5’ represents probability of presence for the species at untreated sites at 0.5 km from water and ‘Yes: 0.5’ represents the respective treatment at 0.5 km from water. the three distance values are 0.5 km from water, 2.5 km from water and 5 km from water. the graphics have been rescaled to be clearly interpreted and therefore probability values are not shown on a full axis (i.e. 0–0.1 probability of presence)

Buffalo

No trends for buffalo were detected at 0.5 km from water (Table 2). In the late dry season, preference was shown for mown plots 2.5 km from water and mown and fertilised plots at 2.5 km and 5 km from water. In the early wet season, preference was shown for mown plots at 2.5 km and 5 km from water. Preference was shown for fertilised plots at 2.5 km and 5 km from water.

No discernible trends for white rhino and elephant could be detected due to their capture frequency (Table 2). Broad models were not robust enough to determine trends.

DISCUSSION

Trade-offs and complex interactions alter how herbivores select for forage at a patch-scale, which consequently affects larger distribution patterns of grazing species. As such, when forage quality and quantity decreases, so does intake rate, resulting in an increase in movement rate (Bailey *et al.*, 1996). Herbivores are able to improve foraging efficiency through spatial memory, allowing them to select more nutritious patches, avoid areas that have little food and remember which resources have recently been depleted (Bailey *et al.*, 1996). These patterns were evident in the utilisation of resources by grazing herbivores in KNP. Each species in this analysis can be considered a representative of functional types, however to avoid over-representing species-specific traits within functional types, these results are discussed by species.

For impala, results indicated that in the dry season they will utilise mown plots closer to water and mown and fertilised plots further from water. The utilisation of resources further from water is likely because in the dry season they will be browsing rather than grazing (Du Toit, 2003), as browse maintains a higher protein content longer into the dry season than grass

(McNaughton & Georgiadis, 1986). Although impala are highly water dependent and typically feed 1-2 km from water (Gaylard *et al.*, 2003), they face trade-offs between browse availability and being close to water in the dry season. Shrub density typically increases with distance from watering points at Satara, with woody vegetation resources having been largely depleted by large herbivores as far as 2.8 km from water (Brits *et al.*, 2002). To overcome this trade-off, they will utilise mown plots in the dry season where they would be able to graze the most nutritious leaves from grass due to their relatively narrow muzzles (Owen-Smith *et al.*, 2017). Impala showed preference for mown and mown and fertilised plots in both the early wet and late wet season, similar to results observed in Hluhluwe-iMfolozi Park, where impala utilise grazing lawns in the wet season and reduce their use going into the dry season (Owen-Smith *et al.*, 2017).

Similarly, wildebeest also use unmown plots closer to water and mown plots further from water, also likely as a result of the trade-offs faced between water dependency and metabolic requirements. Due to their water dependency, wildebeest typically feed 0.5 km to 2 km from water (Gaylard *et al.*, 2003), but unlike mixed feeders they cannot extend this reach in the dry season by utilising browse resources. This could explain their selection for fertilised plots, which would have had higher biomass and higher N content than other mown plots close to water in the dry season. However, in the wet season when water becomes more locally available across the landscape (Gaylard *et al.*, 2003) and grass regrowth is more nutritious after rain (Archibald, 2008), wildebeest show preference for mown and fertilised plots closer to water. Typically, wildebeest are able to exploit short grass resources as a result of their broad muzzle (Arsenault *et al.*, 2008), and will select for these resources of lower structural fiber content (Stock *et al.*, 2010). Overall wildebeest showed low preference for fertilised plots, for which grass heights closer to water remained > 30 cm; and their use of grasses > 21 cm is proportionally much lower than those < 20 cm (Arsenault *et al.*, 2008). The selection of short, low fiber grass in impala and wildebeest improve their digestive rates, allowing them to increase their forage intake (Wirtz & Oldekop, 1991).

In contrast to impala and wildebeest, waterbuck indicated a clear preference for mown plots close to water across all three seasons. Although ruminants, waterbuck are variable grazers (Hempson *et al.*, 2015) and will thus select for grass and other roughage which has the highest available crude protein (Tomlinson, 1980). Grasses typically decrease in crude protein and increase in crude fiber in the dry season (Kutilek, 1979), and waterbuck will alter the forage they select for. This selection is exclusively in the 0.5 km to 2 km zone from water, and our results supported this strong probability of presence only in the 0.5 km zone. Waterbuck are likely competitively displaced by short-grass grazers such as wildebeest and white rhino in the dry season (Cromsigt *et al.*, 2017) when short-grass resources are scarce, and in the wet season on mown and fertilised plots when high densities of impala, wildebeest and zebra select for these resources.

Although zebra are water dependent and typically feed in the 0.5 km to 2 km zone from water (Gaylard *et al.*, 2003), they trade off being close to water to obtain higher quantity of forage in the dry season and periods of drought (Gaylard *et al.*, 2003; Venter *et al.*, 2015). Zebra thus responded to fertilised treatments at all distances from water in the dry season, where grass swards maintained a height of > 50 cm, which zebra typically select for at this time (Arsenault *et al.*, 2008; Sinclair, 1985). Zebra are constrained by metabolic requirements in the dry season and must select for higher quantity forage in order to maintain digestive fill, as hindgut fermenters experience a faster rate of digestive passage (Clauss *et al.*, 2003). In the wet season they typically experience a habitat use overlap with smaller and more selective grazers

(Owen-Smith *et al.*, 2017; Sinclair, 1985) which our results did not indicate at a plot level in the early wet season. However, we did find a preference for mown and fertilised plots further from water in the late wet season. Typically, equids select for heterogenous grazing areas, allowing them to maximise their optimal forage intake by consuming short grass offering high quality and tall grass offering high instantaneous intake rates (Fleurance *et al.*, 2010). This likely explains why we did not detect an overall selection for treated plots, results also found by Owen-Smith *et al.* (2017).

Buffalo trends were difficult to detect and accurately interpret as they may be abundant in biomass but moved through the study area infrequently. They have been shown to select short, high-quality *Cynodon* lawns (for high protein) and taller Sedgelands for bulk intake in Lake Manyara (Prins and Beekman 1989). The selection (fertilized/mown as well as mown) they show in this study could thus be due to them selecting for a more balanced diet.

CONCLUSION

Herbivores form an essential component in the environment in which they occur, due to the impact that they have on their ecosystem. In this paper we aimed to unpack some of the mechanisms behind what affects how herbivores select forage at a patch scale. Results from this study showed that season was a major determinant of species distribution across the landscape, especially those which are not obligate grazers or feed exclusively in the 0.5 km to 2 km zone from water. We found that when freed from the constraints of decreased forage quality and quantity, and limited water availability in the dry season, the probability of presence by species at their preferred forage resource increased. This highlights the trade-off species face under the constraints of the dry season, and species-specific traits which they have adapted to meet metabolic requirements when resources are not readily available (also observed at the landscape-scale, see Young et al. (2019)). Overall, selectivity in larger-bodied species was harder to unravel either due to low camera detection across the sampling period, or their selectivity being at scales greater than what we tested.

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